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The Seafloor Fauna in a Changing Arctic – a Review on Its Past, Present and Future

by Dieter Piepenburg[1]

Abstract: Benthic research in Arctic seas has been intensified since the late 1980s, being considerably promoted by an increased public awareness of the global climate significance of polar regions and the opening of the Russian Arctic to foreign researchers. As a result, our knowledge on the Arctic benthos has been markedly enhanced, leading to the need to revise some widespread concepts about its ecological structure and function, particularly with regard to the often-cited disparities between the Arctic and the Antarctic.
Most generally, the novel data clearly demonstrated that the various Arctic seas differ to a large extent in geographical and environmental setting, impact of fluvial run-off, pelagic production regime, strength of pelagic-benthic coupling and, hence, food supply to the benthos. This spatial variability inevitably results in surprisingly pronounced ecological divergences and impedes all efforts for large-scale generalizations of local and regional findings.
For example, it has been shown that benthos assemblages vary broadly in diversity between Arctic regions, indicating that the idea of a consistently poor Arctic benthos – being in stark contrast to the rich Antarctic bottom fauna – is an undue overgeneralization. In contrast to previous notions, both Arctic and Antarctic waters are, at a biogeographic scale, apparently characterized by intermediate species richness. Levels of disturbance, which are regarded as major determinants of benthic diversity, had been assumed to be relatively high in the Arctic but exceptionally low in the Southern Ocean. The discovery of the great role of iceberg scouring in Antarctic shelf ecosystems, largely overlooked in the past, calls for a reconsideration of this notion.
The great significance of meso-scale features in hydrography and ice cover (marginal ice zones and polynyas) as "hot spots" of tight pelagic-benthic coupling and, hence, high benthic diversity and biomass have recurrently been shown in a number of field studies. In contrast, the importance of terrigenous organic matter discharged to the Arctic seas through fluvial run-off as an additional food source for the benthos is still under debate.
With regard to the deep ice-covered Arctic Ocean, the scientific exploration of which has made particularly great progress in recent years, there is now evidence that its overall productivity has been underestimated by an order of magnitude by previous measurements. As a consequence, the significance of shelf–basin interactions, especially the importance of excess organic carbon exported from productive shelves to the deep ocean, is still debated and, hence, a major topic of on-going research.
The ecological consequences of the rapid warming in the Arctic have been a further research focus of both current and future projects. Most ecological models predict that higher water temperatures, increased fluvial run-off and reduced ice cover will give rise to severe ecosystem changes propagating through all trophic levels. It is hypothesized that there would be a shift in the relative importance of marine biota in the overall carbon and energy flux, ultimately resulting in a switch from a "sea-ice algae – benthos" to a "phytoplankton – zooplankton" dominance.

Zusammenfassung: Die wissenschaftliche Erforschung der Bodenfauna der Arktis ist seit den späten 1980er Jahren verstärkt worden, begünstigt durch das allgemein gestiegene öffentliche Bewusstsein der großen Bedeutung der polaren Regionen für das globale Klima sowie die politische Öffnung der russischen Arktis für ausländische Forscher. Da unser Wissen über das arktische Benthos in der Folge deutlich größer geworden ist, mussten einige weit verbreitete Konzepte über seine ökologische Struktur und Funktion revidiert werden, vor allem im Hinblick auf die oft zitierten Unterschiede zwischen Arktis und Antarktis.
Ganz allgemein haben die neuen Befunde gezeigt, dass sich die verschiedenen arktischen Meeresgebiete deutlich im Hinblick auf die geographischen und ökologischen Rahmenbedingungen, den Einfluss von Flusseinträgen, das pelagische Produktionsregime sowie die Stärke der pelago-benthischen Kopplung und damit die Nahrungsbasis des Benthos unterscheiden. Diese räumliche Variabilität führt unweigerlich zu den überraschend deutlich ausgeprägten ökologischen Unterschieden und erschwert alle Bemühungen, die lokalen und regionalen Ergebnisse großräumig zu extrapolieren.
So konnte zum Beispiel gezeigt werden, dass die Diversität der benthischen Lebensgemeinschaften zwischen den arktischen Regionen deutlich variiert – ein Befund, der zeigt, dass das Konzept eines durchgängig armen arktischen Benthos, das sich vor allem in der Artendiversität von der reichen antarktischen Bodenfauna unterscheidet, eine zu grobe Verallgemeinerung darstellt. Im Gegensatz zu bislang gültigen Vorstellungen sind im großräumigen, biogeographischen Maßstab offensichtlich sowohl arktische als auch antarktische Gewässer gleichermaßen durch einen mittleren Artenreichtum gekennzeichnet. Die Rolle von Störungen, die allgemein zu den wichtigsten Steuerfaktoren der benthischen Diversität gerechnet werden, wurde als verhältnismäßig groß in der Arktis und als ungewöhnlich gering in der Antarktis angenommen. Die Entdeckung der großen ökologischen Bedeutung von strandenden Eisbergen auf den antarktischen Schelfen, die in der Vergangenheit weitgehend unterschätzt worden war, zeigt, dass diese Vorstellung überdacht werden muss.
Durch Feldstudien konnte gezeigt werden, dass mesoskalige Muster in Hydrographie und Eisbedeckung, wie Eisrandzonen und Polynjas, eine große Bedeutung als ökologische „hot spots" haben, die durch eine besonders starke pelago-benthische Kopplung und folglich durch hohe benthische Diversität und Biomasse gekennzeichnet sind. Im Gegensatz dazu ist noch nicht geklärt, wie wichtig terrigene organische Substanzen, die über Flusseinträge in die arktischen Schelfmeere gelangen, als zusätzliche Nahrungsressource für das Benthos tatsächlich sind.
Die wissenschaftliche Erforschung des tiefen zentralen Nordpolarmeers hat in den letzten Jahren besonders große Fortschritte gemacht. Es ist jetzt belegt worden, dass seine Gesamtproduktivität durch ältere Messungen um etwa eine ganze Größenordnung unterschätzt worden ist. Dies hat zur Folge, dass die Bedeutung der Kopplung zwischen den randlichen Schelfen und den zentralen Tiefseebecken, insbesondere die ökologische Rolle des von den produktiven Schelfen in die Tiefsee exportierten organischen Kohlenstoffs, noch umstritten bleibt und deshalb ein wichtiges Thema laufender Forschungsprojekte ist.
Die Abschätzung der ökologischen Auswirkungen der raschen Erwärmung der Arktis ist ein weiterer Schwerpunkt aktueller und geplanter Studien. Nach Prognosen der meisten ökologischen Modelle werden höhere Wassertemperaturen, größere Flusseinträge und geringere Eisbedeckung zu gravierenden Veränderungen in den marinen Ökosystemen führen, die sich auf alle trophischen Ebenen auswirken werden. Eine gängige Hypothese besagt, dass sich die relative Bedeutung der verschiedenen ökologischen Kompartimente im marinen Kohlenstoff- und Energiefluss-Muster verändern wird, was letztlich zu einer Verschiebung in den Dominanzverhältnissen von einem "Meereisalgen – Benthos"-System zu einem "Phytoplankton – Zooplankton" -System führen könnte.

INTRODUCTION

The Arctic has long been considered as a remote and barren place, characterised by extreme environmental conditions, hence inhospitable to man and with only marginal significance for the industrial countries in the temperate regions of Europe, Asia and North America. However, this way of thinking has utterly altered, at latest since the end of the 1980s. It is now commonly acknowledged within the scientific community, and the general public as well, that the high latitudes, especially the ice-covered Arctic seas, are of great global importance as both an indicator and a driver of the emerging large-scale climate changes (MACDONALD 1996, CLARKE 2003). As a result of this attitude shift, which was accompanied by the availability of new research ice breakers and the political opening of the vast Russian Arctic regions to international

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research efforts after a decade-long period of isolation (Piepenburg 1995), the scientific exploration of Arctic seas has been intensified, mostly within the frame of large multidisciplinary projects (Tab. 1). Most of these efforts comprised marine field studies on the benthos of various Eurasian Arctic (Greenland, Barents, Kara, and Laptev seas) and American Arctic seas (Chukchi and Beaufort seas, Baffin Bay). They provided a wealth of novel data, the analysis of which has greatly enhanced our knowledge on Arctic seafloor ecosystems (Piepenburg 2005).

Here, I will give a concise overview of the most salient aspects of this newly gained information on the Arctic benthos. In doing so, I will largely focus on "large" benthic organisms (i.e., the macro- and megabenthos sensu Gage & Tyler 1991) and on off-shore shelf and deep-sea faunas. I do not intend to give a comprehensive review of the current knowledge on Arctic benthos in general but will instead deal with some selected ecological aspects, i.e. those for which the enhanced knowledge collected during the past fifteen years or so strongly suggests to revise some well-beloved common notions about the structure and functioning of high-latitude marine ecosystems. Whenever appropriate, I will contrast Arctic with Antarctic conditions, as the comparative analysis of the similarities and dissimilarities between the two polar systems is particularly suited to deduce general ecological implications (Dayton 1990). Finally, I will demonstrate how the current knowledge allows for posing well-founded hypotheses about the probable development of Arctic marine systems in response to the environmental shifts induced by the emerging global climate change.

GENERAL SETTING

In the following, I use the expression "Arctic seas" in accordance with a widely accepted scheme proposed by Zenkevitch (1963) on the basis of comprehensive studies of the distribution patterns of benthic species: Besides the deep-sea basins in the Arctic Ocean proper as well in the Greenland Sea, this term comprises the waters over the continental margin of Greenland, the Eurasian shelves of the Kara, Laptev and East Siberian seas, the Amerasian Chukchi Sea, the American Arctic shelves of the Beaufort Sea and the Canadian Archipelago (including Baffin Bay), as well as the regions north of the Polar Front of the Barents and Bering seas (Fig. 1).

Arctic seas are generally characterized by very low, but relatively constant water temperatures, permanent or long-lasting seasonal ice-cover, as well as very pronounced seasonal fluctuations in insolation and, hence, primary production (Hempel 1985). However, there are also some ecologically important regional contrasts between the various marginal seas and the Arctic Ocean proper due to differences in geographical position, topography, climate, and hydrography (Curtis 1975, Grebmeier & Barry 1991).

At a geological time scale, the present-day extremely cold climate mode in the Arctic is commonly assumed to having evolved only a rather short time ago, particularly if compared to the Antarctic (Dunbar 1977), where the onset of a significant cooling can be traced back to the Eocene/Oligocene boundary about 40 million years ago (Clarke & Crame 1989). At latest with the opening of the Drake Passage between South America and the Antarctic Peninsula and the formation of the Antarctic Convergence in the early Miocene about 23 million years ago, there was an isolated cold circum-Antarctic Southern Ocean (Thomson et al. 1991). In the northern hemisphere, however, temperate climate conditions prevailed even in polar regions for further 19 million years, i.e., during the entire Miocene (Bleil & Thiede 1990). Current textbook knowledge is that the Arctic Ocean was largely ice-free and had open connections to both the Atlantic and Pacific Ocean until the onset of a drastic global fall of sea temperatures in the Pliocene about four million years ago. However, there is newest palaeoceanographic evidence (Moran et al. 2006) that the first cooling of the Arctic started much earlier, i.e., as early as in the middle Eocene about 45 million years ago, as the first occurrence of ice-rafted debris in a >400 m-long sediment core from the Lomonosov Ridge suggests. Nevertheless, it is undisputed that after the Pliocene cooling a further, very drastic temperature decline happened in the Arctic since the beginning of the Pleistocene 1.8 million years ago. Since then, periodic shifts between "cold" glacial and "warm" inter-glacial climate conditions resulted in the formation of the contemporary setting: a permanently ice-covered central Arctic Ocean fringed by shelf seas with seasonally varying sea-ice cover (Bleil & Thiede 1990).

As a consequence of their geological history, the Arctic shelves are inhabited by a "young" – in evolutionary terms – benthic fauna. As the global sea level varied pronouncedly (>100 m) between glacial and inter-glacial intervals, the shelf regions had repeatedly fallen dry or had, at least partly, been covered by huge glaciers during the Quaternary glacial periods. This means that these areas had to be re-colonized by marine organisms several times during the inter-glacial transgressions following the recurrent Pleistocene glaciations, the last of which ended only about 13,000 years ago (Stein et al. 1994). There is even evidence that substantial erosion by advancing large Eurasian ice sheets also affected greater water depths beyond the shelf break (Spielhagen 2001). These events have very likely led to massive destructions of the marine benthic fauna in wide Arctic areas, particularly on the shallow shelves. Relict populations, which served as seeding sources for the subsequent re-colonization process, must have survived to avoid total annihilation, either in deeper waters or in protected areas where ice scouring was less devastating. The alternating loss and subsequent re-colonization of vast shelf habitats undoubtedly must have had pronounced impacts on the diversity of benthic communities, as well as on the adaptability of benthic organisms.

In addition to such climate shifts on geological time scales, there are also shorter-term environmental variations. During the 20th century surface air temperatures had risen significantly in the Arctic between 1925 and 1945, decreased between 1950 and 1970 and have increased again since 1980 (Lozán et al. 2001). Consequently, the spatial extent and the average thickness of the Arctic pack ice have been reduced by about a third over the last 25 years (Cavalieri et al. 1997, Rothrock et al. 1999). Although it has been recognized that such climate variations follow a cyclic pattern called "Arctic Oscillation" (AO) (Dickson et al. 2000), there is also a consensus that the AO is superimposed to a clear long-term

trend of a general temperature increase (Lozán et al. 2006). Moreover, most predictive models suggest that climate changes will be particularly pronounced in the Arctic, which may warm ~3-4 °C, viz. more than twice the global average, under realistic greenhouse warming scenarios (IPCC 2001). Such changes will not only have direct and easy-to-predict effects on Arctic mammals and sea-ice biota (ACIA 2004) but will most likely also have indirect but severe impacts on both pelagic productivity and organic matter export and will, hence, ultimately also affect benthic communities (Piepenburg 2005).

RAMIFICATIONS OF RECENT FINDINGS

The call for integrated large-scale projects in the Arctic, repeatedly raised in the late 1980s, has indeed been heeded, as the impressive record of such research efforts indicates (Tab. 1). Within almost all these projects, benthic community structure, stock size and distribution patterns were investigated. Regardless of their major research goals, the investigations provided a wealth of novel information, with different implications for common paradigms about the Arctic benthos. Some of those notions were largely supported by the new data – e.g., the concept of an Arctic being characterized by high biogeogra-

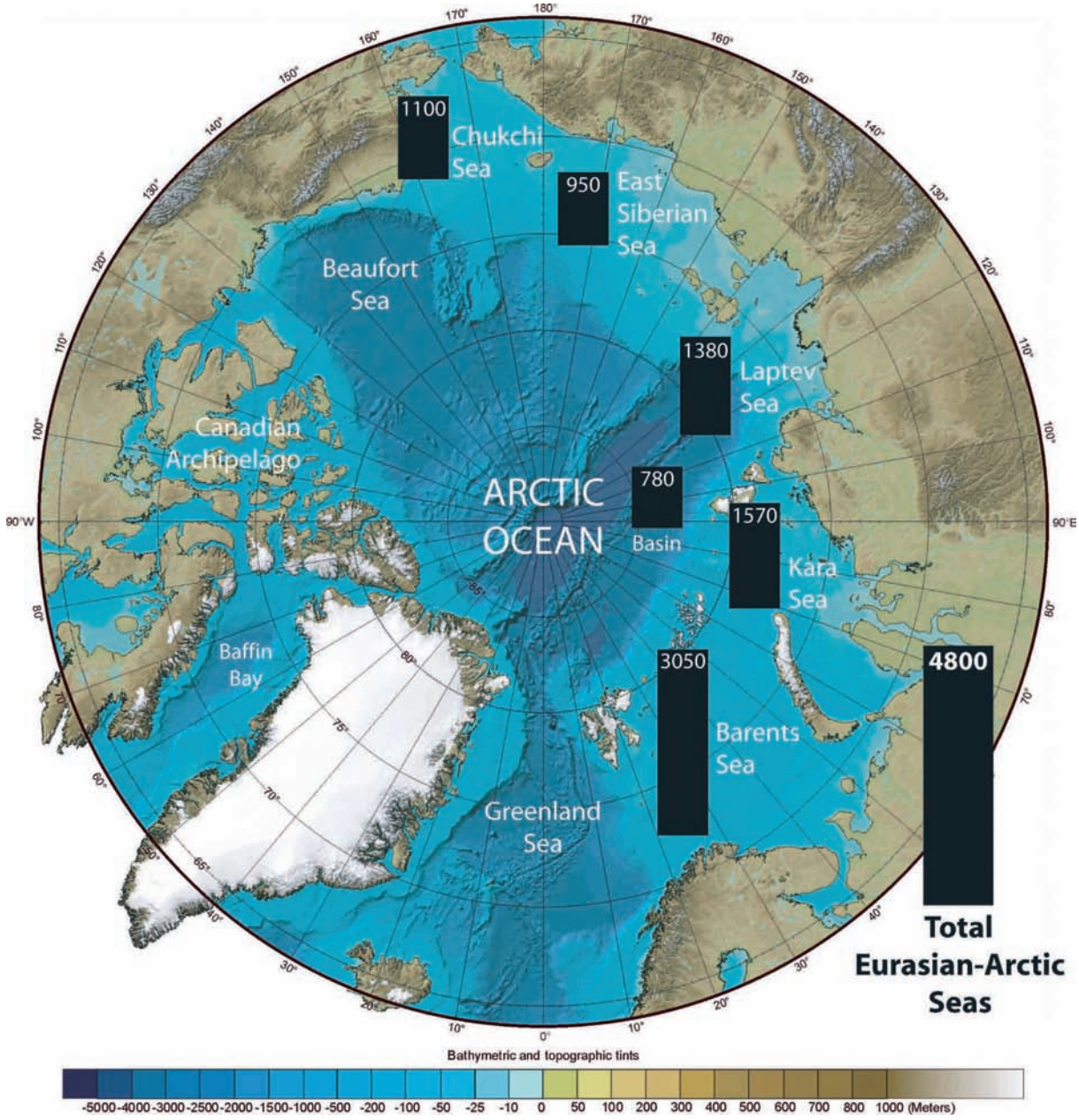

Fig. 1: Distribution of macrobenthic species numbers in the Eurasian Arctic shelf seas and the Eurasian deep basin. Bars represent the number of species that are to date reported to occur in the different regions (data from Sirenko 2001). Map of the Arctic Ocean and its marginal shelf seas is based on IBCAO, the International Bathymetric Chart of the Arctic Ocean; Jakobsson et al. 2001.

Abb. 1: Verteilung der makrobenthischen Artenzahlen in den eurasischen Schelfmeeren und im angrenzenden eurasischen Tiefseebecken. Die Balkenhöhe beschreibt die Anzahl der derzeit bekannten, in den verschiedenen Regionen vorkommenden Arten (Daten aus Sirenko 2001). Karte des Nordpolarmeeres und seiner randlichen Schelfgebiete auf der Grundlage von IBCAO (International Bathymetric Chart of the Arctic Ocean, Jakobsson et al. 2001).

phic affinity to North Atlantic regions (Zenkevitch 1963, Dunbar 1977) and, hence, low degree of endemism (Anisimova 1989, Smirnov 1994) – while others were not, especially those regarding the apparently pronounced difference between Arctic and Antarctic systems (Piepenburg 2005).

Broad regional differences in community patterns

The most fundamental conclusion drawn from the findings of the recent benthic surveys is that there is not just one typical Arctic benthos but a wide variety of communities found in distinct depth zones (shelf, slope, and basin) and regions, which differ profoundly in quite a number of benthic ecology aspects. This variation is caused by differences in water depth, geographical setting, biogeographical history, water current and advection regime, river runoff, ice cover, seafloor composition, and food availability. The ecological effects of these factors are often interrelated (Piepenburg et al. 2001). River runoff, for instance, strongly affects sea-ice dynamics and oceanic circulation pattern, hence pelagic and sympagic productivity regime, and therefore ultimately also benthic food supply. In addition to this important indirect effect, fluvial discharge, as well as coastal erosion, can result in a significant import of suspended inorganic and organic matter, especially in the Siberian marginal seas. The organic matter is subject to various geochemical and biological transformations and might serve as an allochthonous energy source within the marine food webs. Clearly, the knowledge about the quantity, spatio-temporal distribution, and fate of the terrigeneous organic matter is essential for a profound understanding its relevance for the pelagic and benthic systems in the Arctic seas (Fahl et al. 2001). Moreover, the pronounced heterogeneity in environmental conditions and benthic community patterns severely impedes large-scale generalizations of local and regional findings and calls for a pan-Arctic perspective in the pursuit to advance the fundamental understanding of key features of polar marine ecology.

The macrofaunal assemblages in different regions and at different depths are characterized by typical indicator taxa. Shelf regions with fine-grained sandy and muddy sediments, for instance, are often dominated by bivalves and polychaetes (Feder et al. 1994a, Grebmeier & Cooper 1995, Deubel et al. 2003), while gammaridean amphipods are the most prominent faunal elements in coarse-grained sediments (Grebmeier et al. 1995). A general circumpolar pattern in the composition of epibenthic communities is the pronounced numerical importance of brittle stars in Arctic shelf and slope habitats (Starmans et al. 1999, Piepenburg 2000, Sejr et al. 2000, Ambrose et al. 2001). Other conspicuous epifaunal megabenthic elements, which may even exceed the ophiuroid stocks

Title	Acronym	Duration	Region(s)	References/Links
The Northern North Atlantic: A Changing Environment	SFB 313	1985 - 1998	Greenland-Iceland-Norwegian Seas	Schäfer et al. 2001
European Polarstern Study II: Study of the European Arctic Shelf	EPOS II SEAS	1991	Barents Sea	Rachor 1992
AOSB International Arctic Polynya Project	IAPP	1990 - on-going	various Arctic seas	Anonymous 1991 http://www.aosb.org/IAPP.html
Northeast Water Polynya Study	NEW	1992 - 1993	Greenland Sea	Hirche & Kattner 1994
North Water Polynya Study	NOW	1997 - 1999	Baffin Bay	Deming et al. 2002 http://www.fsg.ulaval.ca/giroq/now/
AOSB Shelf-Basin Exchange Initiative	SBE	2001 - on-going	various Arctic seas	http://www.aosb.org/SBE.html
System Laptev Sea		1993 - 2002	Laptev Sea	Thiede et al. 1999
Siberian River Run-Off	SIRRO	1997 - 2003	Kara Sea	Stein et al. 2003 http://www.awi-bremerhaven.de/GEO/SIRRO/
Western Arctic Shelf-Basin Interactions	SBI	1998 - on-going	Beaufort Sea Chukchi Sea	Grebmeier 2003 http://sbi.utk.edu/
Canadian Arctic Shelf Exchange Study	CASES	2002 - on-going	Beaufort Sea	Louis Fortier, pers. comm. http://www.cases.quebec-ocean.ulaval.ca/
Carbon Flux and Ecosystem Feedback in the Northern Barents Sea in an Era of Climate Change	CABANERA	2002 - on-going	Barents Sea	Paul Wassmann, pers. comm. http://www.nfh.uit.no/cabanera/

Tab. 1: Recent (those terminated after 1990) and current research efforts in Arctic seas. This lists comprises projects, in the frame of which benthic field studies have been conducted during the past two decades. AOSB = Arctic Ocean Sciences Board.

Tab. 1: Kürzlich (d.h. nach 1990) abgeschlossene und laufende Forschungsprojekte in arktischen Meeresgebieten. Diese Liste enthält Projekte, in deren Rahmen in den letzten zwanzig Jahren benthische Feldstudien durchgeführt worden sind. AOSB = Arctic Ocean Sciences Board.

in terms of biomass, are sea urchins in the Barents Sea (Bluhm et al. 1998), sea cucumbers and bivalves in the Laptev Sea (Piepenburg & Schmid 1997), as well as sea stars and crustaceans in the Bering and Chukchi seas (Jewett & Feder 1981, Feder et al. 2005).

A pronounced depth zonation in the composition and distribution of benthic assemblages, accompanied by an exponential decline of benthic standing stock along a shelf-slope-basin gradient, is a common phenomenon in Arctic seas (Curtis 1975), as well as it is world-wide (Rowe et al. 1974, Haedrich et al. 1980, Stewart 1983, Lampitt et al. 1986, Brey & Clarke 1993, Dahm 1996). The ultimate cause of this ubiquitous pattern is difficult to assess. Any zonation observed must very likely be viewed as the result of not just one single factor but of several direct and indirect processes operating on various spatial and temporal scales (Carney et al. 1983). Hydrostatic pressure, the factor directly related to water depth, has been shown to cause specific physiological adaptations of the organisms (Somero et al. 1983) but it is regarded to be of only marginal significance for explaining the large-scale (100-1000 km) depth zonation in composition and standing stock of benthos assemblages (Somero 1990). Results from many field studies rather suggested that this is primarily caused by gradients in food availability and seabed properties. Both determinants are known to be strongly related to water depth, hydrodynamics and various processes of particle transport, such as turbidity plumes, Taylor columns and internal waves. There is a general inverse relationship between sedimentation rates and water depths (Suess 1980, Martin et al. 1987), which explains the fundamental influence of water depth on the quality and quantity of organic carbon reaching the sea floor and, hence, on the food supply for the benthos (Graf 1992). In energy-limited systems, such as the deep sea or polar seas, food supply has frequently been proposed as the prime agent controlling meio-, macro- and megabenthic biomass, being more important than physiological adaptations, biological interactions or competition for space (Hessler & Jumars 1974, Rowe et al. 1974, Lampitt et al. 1986, Grebmeier & Barry 1991). The novel results were consistent with this chain of arguments, which points to the special significance of the pelagic-benthic coupling for the benthos in Arctic waters.

Diversity and disturbance

A key question of a large number of polar benthic studies is whether the Arctic has a lower diversity than regions in lower latitudes or the Southern Ocean. Concerning large-scale (i.e. biogeographical) species richness, which is least susceptible to bias by systematic errors, the common notion fifteen years ago was clear (Knox & Lowry 1977): with regard to most taxa, Arctic seas harbour markedly less species than other regions of comparable size. However, recent studies have provided some contrary evidence that definitely calls for caution when addressing the issue posed above. While for some taxa the hypothesis of an impoverished Arctic has been corroborated, e.g., for brittle stars (Piepenburg 2000), the picture is not that clear-cut for the benthos as a whole. Sirenko & Piepenburg (1994) reported a total of more than 4000 macrozoobenthic species for the entire Eurasian Arctic. Seven years later, Sirenko (2001) listed about 20 % more species, i.e., a total of about known 4800 species for the entire Eurasian Arctic and a total of about 800 for the deep Eurasian basins of the Arctic Ocean – a region that was almost unknown fifteen years ago but has since been investigated in a number of studies. Sirenko (2001) also demonstrated that the benthic diversity varies broadly among Arctic regions (Fig. 1), ranging from the Barents Sea (3050 species) to the East Siberian Sea (950 species). There is thus a clear decrease in species richness from west to east, generally corroborating previous findings already reported by Zenkevitch (1963). However, it should be noted that this trend is very probably caused by at least two factors: on the one hand it reflects a true zoogeographic pattern shaped by differences in climate, geographic position and immigration rates of Atlantic and Pacific immigrants, on the other hand it is also influenced by the fact that the regions have not been investigated with comparable effort (e.g., since decades the Barents Sea has been much more thoroughly studied than the East Siberian Sea). In general, all diversity inventories are biased to a considerable degree by a host of methodological factors (e.g., differences in sampling intensity and spatial scales covered) – a fact that makes any comparison of species richness rather problematic (Hurlbert 1971). However, it can safely be concluded that the clear increase in the overall number of known species, which is primarily due to recent research efforts such as the 10-year Russian-German Laptev Sea Study (Kassens et al. 1999), indicates that the species inventory of the Arctic seas is probably not complete yet.

The same conclusion applies to the Southern Ocean, for which Arntz et al. (1997) and Clarke & Johnston (2003) reported the number of all known macrozoobenthic species to range between 4100 and 5000. Gutt et al. (2004) reckon that these figures underestimate the real species number by more than 100 % and estimate that between 11000 and 17000 macrozoobenthic species inhabit the entire Antarctic shelf. Analogous approximations for the Arctic seabed fauna are not available to date. Comparing the current state of knowledge on large-scale species richness, Gutt et al. (2004) concluded that the number of macrozoobenthic species in the Antarctic seems to be indeed higher than in the Arctic, but to a much lesser degree than previously thought.

Other large-scale biomes harbour pronouncedly more (10-20 times) species. The world-wide number of known-to-science species occurring in coral reefs has been estimated to total 66000 (Reaka-Kudla 1997), and more than 10 times of this number, about 670,000 species, are expected to be the tally after a complete inventory (Reaka-Kudla 1997). From the deep sea as a whole, May (1992) reported about 250,000 macrofauna species as being currently recorded, and the estimates of the true species number range widely between about 500,000 (May 1992) and 10,000,000 (Grassle & Maciolek 1992). Although these numbers are rather rough approximations, it is clear that, at a global scale, both Arctic and Antarctic seas are characterized by only intermediate species richness – a notion that is clearly different from the old paradigm of a very poor Arctic versus a rich Antarctic benthos.

Diversity has repeatedly been shown to be closely related to "stability" and "disturbance". Both these terms are not very clear ecological concepts, and there are a number of different definitions (Pickett & White 1985). Dayton (1990) and

Grebmeier & Barry (1991) have emphasized the great significance of disturbance as a key determinant of Arctic benthic shelf assemblages. They argued that crucial benthic community features, such as diversity, biomass and productivity, vary remarkably in response to disturbance levels. In general, these levels are supposed to be comparatively high in Arctic seas – due to physical disturbances (ice gouging, freshwater and sediment input leading to variable salinities and high turbidity levels, variable ice cover), biological disturbances (feeding activities of invertebrate predators, such as gastropods, ophiuroids, asteroids and crustaceans, as well as marine mammals, such as grey whales and walruses), and progresssively more also anthropogenic disturbances (Jewett et al. 1999). Such high disturbance levels are assumed to limit overall benthic diversity. In contrast, Antarctic shelves have been thought to be characterized by markedly lower disturbance levels that enable benthic communities to reach high species diversities (Dayton 1990).

However, the concept of an "unstable and, hence, poor Arctic benthos versus a stable and, hence, diverse Antarctic benthos" is too simple, as results from recent research work strongly suggest. There is now good evidence that grounding icebergs or deep pressure keels of drifting sea ice exert catastrophic disturbances on benthic habitats, in both the Arctic (Conlan et al. 1998), where they can – in addition to their abrasive primary effect – lead to local hypoxia at gouged seabed patches (Kvitek et al. 1998), and the Antarctic (Peck et al. 1999). Moreover, Gutt (2001) showed that in the Antarctic Weddell Sea iceberg groundings apparently happen much more often and affect much larger seabed areas than previously thought.

Like other discrete catastrophic events in other biomes, such as forest fires, tree falls or hurricanes, ice scouring is now recognized to be fundamental to the functioning of the entire Antarctic shelf ecosystem, as their disastrous initial impact is followed by positive effects on biodiversity (Gutt & Piepenburg 2003). Novel findings suggest that two processes, operating on different spatial and temporal scales, regulate the diversity of Antarctic shelf benthos. In accordance with the "stability-time hypothesis" (Sanders 1968), the high local diversity of undisturbed Antarctic shelf benthos is primarily the result of the evolution of sponge-dominated assemblages over long and stable time spans. However, in accordance with the "intermediate disturbance hypothesis" (Huston 1979), the diversity on regional scales – possibly even that on a larger scale encompassing the entire Antarctic shelf (<300 m) – is strongly influenced by catastrophic iceberg disturbances. Grounding icebergs in both the Arctic and Antarctica – and, at the shallow Arctic shelves, grounding pressure-ice-keels of drifting pack ice – devastate large seabed patches and virtually eradicate the benthos at these places. However, after being released, they leave behind free seafloor space that can be recolonized. Over a longer time span and at a regional scale, iceberg groundings positively affect the spatial and temporal habitat diversity and prevent the competitive displacement of species, which is characteristic for undisturbed systems near the ecological equilibrium and results in a reduction of diversity. They create a mosaic of habitats in different succession stages and thus enhance between-habitat and, hence, regional diversity (Gutt & Piepenburg 2003).

In addition, indirect disturbance effects of iceberg or sea-ice scouring, such as changes of small-scale bottom-water current regime or modification of small-scale seabed topography, have further ecological consequences, which may be even more far-reaching and, hence, possibly even more significant than the initial mechanical habitat destruction through the abrasion of large seabed patches (Piepenburg 2005).

Pelagic-benthic coupling as an ecological key process

Dayton (1984) pointed out that benthic distribution and community features, such as composition, diversity, and standing stock, are influenced by a complex of abiotic and biotic factors and processes, e.g., water depth, habitat heterogeneity, sea-floor properties, bottom-water hydrography and current regime, food availability, as well as inter- and intraspecific competition and disturbance caused by predation or burrowing activities (Gray 1981). They interact within a complex network of relationships (Dayton 1984), and their relative importance does strongly depend on the spatial scale considered (Dayton & Tegner 1984, Gage & Tyler 1991). Seabed attributes are usually most significant at small (i.e., local) scales (Snelgrove & Butman 1994), while the quantity, quality and temporal pattern of food supply seems to primarily regulate the benthic distribution and stock size at larger (i.e., regional) scales (Dayton & Oliver 1977, Graf 1992).

In general, the food supply of the vast majority of benthic biota depends entirely on the import of organic matter originating from the autotrophic production in the upper euphotic layer of the water column (Tyler 1995). There are prominent exceptions from this rule, e.g., littoral habitats at comparatively little water depths, to which sufficient sunlight can penetrate to allow for benthic primary production, or the chemosynthetic communities found at hot vents (Grassle 1986, van Dover 2000) and cold seeps (Sibuet & Olu 1998). At a global scale, however, these biota are of only minor significance in spatial extent and overall energy turnover. The downward flux of matter and energy from the water column to the seabed is the most important aspect of the crucial relationship between the pelagic realm and the benthos, for which the term "pelagic-benthic coupling" has been coined (Hargrave 1973). The food supply to the benthos, hence the import of allochthonous organic matter from the water column, strongly affects a wide range of benthic patterns and processes, including biogeography, diversity, population densities, biomass and activity of the seafloor fauna. Consequently, the benthos is strongly influenced by abiotic and biotic water-column processes controlling the pelagic production as well as the downward flux (sedimentation) of organic matter to the seabed (Grebmeier & Barry 1991, Graf 1992).

In Arctic seas, pelagic production and sedimentation of organic matter vary considerably among the various regions as a consequence of the effects of different promoting / impeding processes (Sakshaug 2003). In general, these processes are strongly affected by sea-ice (Honjo 1990, Smith & Sakshaug 1990). Furthermore, sea-ice algae can contribute considerably to the total productivity of polar seas (5 to >33 %; Legendre et al. 1992). Therefore, the spatio-temporal pattern of sea-ice cover influences, via the pelagic-benthic coupling, the trophic basis of seabed communities and has to be regarded as another

important control agent of benthic systems, particularly for those on the shelves of Arctic and Antarctic seas (Grebmeier & Barry 1991, Arntz et al. 1994).

At high latitudes, the strength of pelagic-benthic coupling and, hence, food supply is regarded to be of particular importance for the benthos. Clarke (1983) claimed that the amount of sedimenting food particles rather than the low temperatures *per se* control the metabolism, growth and survival of polar benthic organisms. Petersen & Curtis (1980) stated that, for similar depths and substratum types, benthic biomass seems to be greater in the Arctic than in boreal or tropical areas. Based on this observation, Petersen (1984) suggested a general increase in the efficiency of energy transfer between water column and seabed – and, thus, significance of pelagic-benthic coupling – with increasing latitude. This pattern was assumed to be primarily caused by a generally reduced zooplankton grazing pressure and, hence, enhanced sedimentation rates of ungrazed organic matter to the seabed, resulting from the greater time lag in the response of zooplankton populations to the high seasonal oscillations in phytoplankton production at higher latitudes (Petersen & Curtis 1980, Schnack-Schiel & Isla 2005). This concept has been corroborated by the findings of a number of pelagic sedimentation studies, indicating that at higher latitudes a progressively larger proportion of the organic carbon fixed in the euphotic zone falls to the sea floor (Wassmann et al. 1991). Therefore, the benthos in Arctic and Antarctic waters has been postulated to have a greater role in the marine carbon production and turnover regime than at lower latitudes (Petersen 1984). As a consequence, the substantial benthic biomass accumulated in some areas supports major feedings grounds of resident and migrating sea birds (Gould et al. 1982) and mammals (Highsmith & Coyle 1990, 1992).

However, Grebmeier & Barry (1991) demonstrated that the significance of the pelagic-benthic coupling varies broadly among Arctic seas, ranging from high in biomass-rich areas to rather low in poor food-limited regions, and advised against making too broad generalizations. According to Grebmeier & Barry (1991), in most Arctic and Antarctic regions a large amount of the organic matter produced in the upper water column or the sea ice is consumed by zooplankton or recycled via the microbial loop before it reaches the seabed, resulting in generally food-limited regimes for the underlying benthos. However, some continental shelves, such as those in the Bering, Chukchi, and Barents seas, where a tight coupling between pelagic / sympagic primary production and benthic secondary production causes high benthic standing stocks, are exceptions from this general pattern.

Moreover, it has been demonstrated that there are prominent "hot spots" of tight pelagic-benthic coupling in both polar regions. These are certain meso-scale patterns in hydrography and sea-ice cover, which regionally enhance pelagic and / or sympagic primary production and the food supply to the benthos and, hence, have obviously a great impact on benthic spatial distribution patterns. For instance, marginal ice zones (MIZ) are such well-known sites of locally and temporally increased production in Arctic and Antarctic ice-covered seas (Slagstad 1985, Sakshaug & Skjodal 1989, Niebauer 1991, Wassmann et al. 1991, Savidge et al. 1996). In particular "seasonally receding ice edges", as they are found in the northern Barents Sea (Loeng 1989) and in the Laptev Sea (Timokhov 1994), induce prolonged diatom blooms by favourable modifications of the local hydrography (Rey & Loeng 1985, Smith & Nelson 1985). Moreover, several sediment trap studies in both Arctic and Antarctic waters have demonstrated that a large amount of the organic matter produced in the MIZ tends to sink out of the euphotic layer in strongly pulsed sedimentation events (Honjo 1990, Hebbeln & Wefer 1991, Bauerfeind et al. 1994, Andreassen et al. 1996) and is, thus, exported as potential food for the benthos (Schewe & Soltwedel 2003). Not surprisingly, MIZs are known as regions of high benthic standing stocks (Grebmeier & Barry 1991, Piepenburg 2000).

A second type of "hot spots" are polynyas. These are permanent or recurrent ice-free areas in polar pack-ice zones, which have been identified to be of special importance for both physical and ecological processes (Stirling 1980, Smith et al. 1990, Gradinger 1995, Grebmeier & Cooper 1995). Pronounced meso-scale gradients characterize their hydrographic regimes (Schneider & Budéus 1994). Compared to surrounding ice-covered areas, pelagic production is often relatively high (Gradinger & Baumann 1991). Field studies in the Northeast Water (NEW) polynya off Northeast Greenland demonstrated a tight pelagic-benthic coupling. Results of isotope studies suggested that fresh ungrazed organic carbon reaches the sea bed below the polynya (Hobson et al. 1995), presumably due to low levels of zooplankton grazing (Hirche et al. 1994, Ashjian et al. 1995, 1997, Hirche & Kwasniewski 1997), and benthic abundance and biomass were reported to be considerably higher than in adjacent ice-covered regions (Ambrose & Renaud 1995, Brandt 1995, Piepenburg & Schmid 1996b). Similar conditions have been described for an area in the Bering Sea influenced by the St Lawrence Island polynya in winter / spring (Grebmeier 1993, Cooper et al. 2002). For the Laptev Sea, there is evidence that endobenthic biomass (Gukov 1995) as well as brittle star stocks (Piepenburg & Schmid 1997) are positively influenced by the spring flaw-lead off the coastal fast-ice belt. In general, high Chl *a* concentrations in the sediments indicated a tight coupling between sympagic and pelagic primary production and food supply to the benthos throughout the entire Laptev Sea shelf (Schmid et al. 2006).

All this convincing evidence of the great significance of pelagic–benthic coupling and food supply for the benthos does, of course, not mean that the organic matter sustaining the bottom fauna originates exclusively – or even primarily – from the primary production in the overlying waters. Allochthonous organic matter advected from adjacent more productive areas has repeatedly been shown to be an additional major food source of benthic communities in comparatively unproductive high-Arctic seas (Grebmeier 1993, Feder et al. 1994a, b, Feder et al. 2005). In the Barents Sea, for instance, the southward inflow of Arctic surface water is thought to be counterbalanced by a northward transport of warmer but more saline Arctic-Atlantic bottom water formed mainly at the Polar Front (Loeng 1989). These water masses are supposed to carry organic matter produced in the more productive southern Barents Sea to the north (Piepenburg & Schmid 1996a). In the northeastern Chukchi Sea, the advection of allochthonous particulate organic carbon (POC) helps to sustain a biomass-rich population of benthic ampeliscid amphipods that serves

each summer as the main food resource of migrating bottom-feeding grey whales (Feder et al. 2005). In general, the great significance of lateral advection for the dispersal of organic carbon in the benthos is indicated by the fact that the benthic carbon demand is only rarely matched by the carbon supply via sedimentation out of the overlying water column estimated from sediment-trap data (Christensen 2000).

Terrigeneous production, reaching the sea primarily through fluvial transports, is another source of allochthonous food for the benthos. This source of organic carbon might be particularly important in the Arctic, as about 10 % (viz., about 3500 km^3 $year^{-1}$) of the global river run-off enters the Arctic seas and leads to a strong coupling between terrestrial and marine ecosystems (Klages et al. 2003). Especially the Laptev Sea is heavily affected by fluvial inflow (Timokhov 1994), with the Lena river being estimated to discharge about 5.3 x 10^6 tons of organic carbon each year, most of it during the flood period in June/July (Cauwet & Sidorov 1996). Schmid et al. (2006) provide evidence that autochthonous primary production might not be sufficient to sustain both pelagic and benthic secondary production in the Laptev Sea, implying that an input of allochthonous organic carbon is required to balance the overall carbon budget. However, most of the imported fluvial organic matter is fairly degraded (Stein 1996, Fahl et al. 2001) and, thus, of probably rather poor nutritional quality. Therefore, its actual significance as food source for the bottom fauna is difficult to be estimated but is commonly assumed to be rather small (Klages et al. 2003).

The deep Arctic Ocean and the role of shelf–basin interactions

The most obvious progress in the past two decades has been made in the scientific exploration of the deep ice-covered Arctic Ocean, which was largely unknown before, as a number of quantitative studies have provided novel information on the benthos of the Amerasian and Eurasian basins (Kröncke 1994, 1998, Clough et al. 1997, Soltwedel & Schewe 1998, Schewe & Soltwedel 1999, Deubel 2000, Kröncke et al. 2000, Vanreusel et al. 2000, Bluhm et al. 2005). The Arctic Ocean proper is unique in its physical and biological properties. It is characterized by the most extreme limitations in solar radiation and nutrient availability, permanent ice cover and temperatures always close to the freezing point – a combination of factors with a very negative effect on overall biological productivity. Consequently, the Arctic Ocean has long been considered to be one of the least favourable habitats for life on Earth and, hence, the poorest – in terms of both diversity and productivity – part of the world's ocean. This notion is still not totally false but novel findings have called for a rectification of the estimates of annual (particulate) primary production by one order of magnitude (from 2 to 15-30 g C m^{-2} $year^{-1}$; MacDonald & Carmack 1991, Macdonald et al. 1993, Wheeler et al. 1996, Gosselin et al. 1997, Sakshaug 2003).

The recent benthos investigations largely confirmed the expectation that species richness, abundance and biomass decrease quite steeply along a shelf-basin gradient with water depth and latitude (Kröncke 1994, 1998, Clough et al. 1997, Deubel 2000, Bluhm et al. 2005). They are generally at rather low levels (5 to 500 species m^{-2}, 5 to 6625 individuals m^{-2}, and 5 to 130 mg C m^{-2}), lying at the lower margin of values reported from the deep basins of the North Atlantic (Levin & Gooday 2003). These findings corroborated the notion that the major factor affecting the Arctic deep-sea benthos is energy limitation caused by very limited organic matter supply to the abyssal seafloor.

Benthic carbon mineralization rates range from 1 to 10 g C m^{-2} $year^{-1}$, i.e., they are one order of magnitude lower than Arctic shelf values but by all means comparable to other oligotrophic oceanic regions (Klages et al. 2003), and recent foraminiferal investigations have revealed that benthic communities in the deep basins of the Arctic Ocean are driven by the sedimentation of fresh organic material (Kröncke et al. 2000). These findings imply that the autochthonous production in the Arctic Ocean, albeit being rather low, may be sufficient to nourish the underlying benthic deep-sea communities (Klages et al. 2003). This conclusion is contradictory to the notion that the Arctic deep-sea benthos relies trophically on the import of organic carbon from productive Arctic shelf regions (Grebmeier 2003). The finding that bacterial biomass and activity does not decrease along a bathymetrical and latitudinal gradient to the North Pole rather suggests that it is largely decoupled from the production on the adjacent marginal seas (Klages et al. 2003). Although there is also some evidence of lateral transport from terrestrial, coastal, and shelf sources to the central Arctic Ocean, the supply of utilizable carbon, feeding the abyssal benthic communities, apparently depends very much on the vertical flux of organic matter to the seabed, either from overlying pelagic / sympagic production or in the form of large food falls (Klages et al. 2001, Soltwedel et al. 2003). Klages et al. (2003) conclude that additional food imported from the shelves does not seem to be necessary to meet the deep-sea benthic carbon demand in the Arctic Ocean.

In general, continental shelves are regions that are characterized by strong lateral exchanges of heat and matter between both each other and adjacent deep-sea regions. These transport processes include the export of organic carbon, as the shelves are usually much more productive than oceanic areas and, hence, excess production is available. The significance of organic matter transport from the shelves across ocean margins to the deep sea has been the topic of several oceanographic programmes in the past 20 years in temperate seas (e.g., Walsh et al. 1988, Buscail et al. 1990, Biscaye et al. 1994, Blake & Diaz 1994). A general outcome of these studies was that the lateral input of biogenic detritus at the slope is usually so high that it causes an enhanced activity and abundance of benthic organisms at depth (Anderson et al. 1994, Kemp 1994, Rowe et al. 1994).

It has been hypothesized that such shelf-basin interactions might be particularly intense in the Arctic, as the deep central basins are nearly landlocked and surrounded by large marginal shelves, some of which are quite productive (Grebmeier 2003). In addition, some shelves receive significant imports of freshwater and matter, including terrigenous and fluvial carbon, from several major rivers, leading to a strong coupling between the terrestrial and marine environment, especially in the estuaries and shallow shelves but also in the entire Arctic in general (Macdonald 2000). The total freshwater discharge is large enough to generate the overall estuarine circulation of the Arctic Ocean and, hence, riverine and terrigenous carbon

can be expected to contribute significantly to the possible export of organic material from the shelves to the central Arctic (Grebmeier 2003).

It has been shown that Arctic marginal shelves indeed export both dissolved and particulate organic carbon to the central basins (Stein & Macdonald 2003). However, it is still not clear of what nutritional quality and how significant the quantities of POC exports are. The terrigenous and fluvial POC has already undergone significant biological degradation during its passage through the rivers and the coastal seas, and their suitability as food is thus presumably rather low (Stein 1996, Fahl et al. 2001). Consequently, these materials may be used to track processes involved in long-term burial in the sediments rather than as a substantial supply of usable organic matter to benthic communities (Klages et al. 2003). In quantitative terms, the export of shelf POC probably depends very much on the shelf width (Christensen 1989): narrow shelves tend to export a large proportion of their production while at wide ones most carbon is retained in the shelf system and only a rather small part is exported. As many Arctic shelves, such as the Barents Sea, the Siberian marginal seas, and the Chukchi Sea, are among the widest shelf regions in the world, exceeding up to 800 km from the coast to the shelf break, most organic carbon may be trapped on the shelves and the central Arctic Ocean may receive only a small magnitude of shelf or terrestrial carbon. Lisitsin (1995) provided evidence for this hypothesis, as he has shown that 90-95 % of the suspended matter is deposited on the shelf of the Kara Sea south of 74 °N. The Beaufort Sea shelf, however, is rather narrow and, hence, may well be a source of sediments, nutrients, organic matter and organisms exported to the Arctic Ocean (Grebmeier 2003). In conclusion, the role of shelf-basin interactions for the food supply of Arctic abyssal benthos and in the overall Arctic carbon cycle remains an open issue of current and future research.

Possible ecological effects of climate change

The study of the ecological effects of the pronounced climate change in the Arctic has been – and will remain – a major theme of recent, current and future research projects. It is now commonly accepted that the Arctic Ocean is the region where changes in climate, hydrography and ecology, related to global warming, can be expected to be strongest and, hence, the Arctic can serve as a "harbinger of global change" (IPCC 2001, ACIA 2004). The vast Arctic shelves are likely to be particularly sensitive because of their comparatively low depth, seasonally varying ice cover, and dependence upon inflowing waters from the oceans and continents to the south. On the other hand, as just these Arctic systems are thought to be characterized by a variety of natural disturbances and have been subjected to pervasive environmental shifts in the past, they might be particularly well adapted to extreme climatic variations in terms of resilience (Dayton 1990).

Recent studies have shown that deep Arctic Ocean temperatures have increased over the past 30 years (Dickson 1999). Global change will lead to further rapid increases of air and water temperatures, probably being two times higher than for the rest of the world (ACIA 2004). In addition, it will also affect the freshwater runoff of Arctic rivers (Peterson et al. 2002) and, hence, the production of sea ice. Warming will remove ice, whose annual cycle of melting and freezing structures the varying pan-Arctic rates of shelf exchange with the central basins. Reduced sea-ice coverage will lead to lower cloud cover (due to less cold condensation), a lower albedo (which has in turn a positive feedback on sea ice reduction), and possibly a higher primary production, resulting in a higher removal of atmospheric CO_2 and increased sequestration of carbon on the Arctic shelves. In addition, a possible decrease in stratification would also bring warmer water to the surface.

Even given the proposed resilience and adaptability of Arctic systems in general (Dayton 1990), a climate change being so drastic that it results in a shift from a "cold / abundant ice" to a "warm / limited ice" mode will probably have profound ecological consequences propagating through all trophic levels, as sea-ice dynamics is the prime physical factor driving marine Arctic biology from cellular physiology and biochemistry to food-web and habitat structure (ACIA 2004). It is clear that the effects will be most direct and severe for sympagic and pelagic biota near the ocean-atmosphere interface. Sea-ice assemblages, as well as organisms that directly or indirectly depend on their productivity such as ringed seals and polar bears, are acutely threatened by the rapid reduction of the habitat they rely on (Born 2006). In contrast, other species, such as invaders from boreal regions, are likely to benefit from the rise of sea temperatures and extend their biogeographic distribution range to the north (Berge et al. 2005, Grebmeier et al. 2006). Overall, the ecological effects are assumed to be not as pronounced for the benthos, but because of the pelagic–benthic coupling the profound environmental changes at the sea surface and in the upper water column will ultimately also affect the seabed communities.

In view of the rigour of the expected effects, studies on the supposedly substantial ecological consequences of climate change in the Arctic are regarded to be of high importance (ACIA 2004). However, their number, especially those with explicit reference to the benthos, is actually rather scarce. Because of the time scales involved, the response and adaptability of macrobenthic organisms to changing environmental conditions can hardly be examined directly and, hence, have to be deduced from time-series data of community parameters such as diversity, distribution patterns and composition of benthic assemblages. An example of this kind of studies is a comparison of epifaunal standing stocks in the southeastern Chukchi Sea (Feder et al. 2005). The results suggested that overall community structure did not change from 1976 to 1999, but some dominant taxa were clearly more abundant and had higher biomass in the more recent surveys. However, findings like this should be interpreted with due caution, as they cannot unambiguously be related to regime shifts caused by the general warming of the Arctic (Feder et al. 2003). There is good evidence from comparative studies, however, that the diversity of Arctic fjord communities will decline in response to the climate-induced retreat of glaciers and the resultant increase in mineral sedimentation from melt waters (Wlodarska-Kowalczuk & Weslawski 2001). In the northern Bering Sea, a major ecosystem shift in response to increased air and sea temperatures and reduced sea-ice cover has been observed over the past decade, involving a geographic displacement of marine mammal population distribution, reduction of benthic prey populations, and an increase of

pelagic fish (Grebmeier et al. 2006). And from "Hausgarten", a long-term deep-sea observatory erected in 1999 in the eastern Fram Strait at 2600 m depth Soltwedel et al. (2005) reported data suggesting a decreasing flux of phytodetrital matter to the seafloor and, subsequently, a decreasing trend in sediment-bound organic matter and total microbial biomass in the sediments. It is difficult, of course, to distinguish between changes due to natural variability on multi-year time scales (in relation to the Arctic Oscillation) and those caused by lasting climate shifts. However, the results of oceanographic measurements (Schauer et al. 2004) suggest that the changes observed by Soltwedel et al. (2005) are correlated with – and thus may be caused by – a clear warming trend in the deep water of the Fram Strait.

Summarizing the hitherto existing evidence in a conceptual model, which is intended to provide a common framework for future research efforts, it is hypothesized that upon warming the relative importance of sea-ice biota, pelagic communities and benthic assemblages will shift from a "benthos-dominated" to a "zooplankton-dominated" mode – a process that will fundamentally change the general pattern of kryo-pelagic-benthic fluxes of matter and energy in Arctic seas (Carroll & Carroll 2003). Such a persistent change in the pelagic regime of primary and secondary production would most likely lead to profound changes in species composition, productivity and standing stocks of Arctic benthos and marine mammals. In general, there would be a shift in the relative importance of sea-ice, pelagic and benthic biota in the overall carbon flux from a "sea-ice algae–benthos" to a "phytoplankton–zooplankton" dominance (Fig. 2; Carroll & Carroll 2003). Although the average primary production is expected to rise from about 50 to about 100 g C m^{-2} $year^{-1}$, mainly because of the extension in the duration of the growing season and the northward shift of high-productions zones (fronts, MIZ), the predicted increase in zooplankton grazing would result in a reduced flux of POC to the seabed and, consequently, decreased benthic biomass. And in fact, there is current evidence that such a fundamental alteration also has a negative impact on large marine carnivores (seabirds and sea mammals) and favours smaller carnivores (pelagic fish) because of a significant drop in the average body size of prey species, as it has been observed in the Barents Sea (Karnovsky et al. 2003) and the Bering Sea (Grebmeier et al. 2006). Other scenarios, however, predict that the expected increase in overall primary productivity in the Arctic will not only be positive for the pelagic biota but for the benthos as well, particularly on the shallow shelves near the coasts where low water depths result in a particularly strong pelagic–benthic coupling (Piepenburg & Gutt 2006). Such a development might be thwarted by the invasion of species from lower latitudes as a consequence of the probable northward range extension of boreal species. One far-reaching ecological effect may be a considerable increase in the predation pressure to benthic invertebrate populations due to the feeding activities of abundant demersal fish species, such as cod, that are currently restricted from high-Arctic regions. Besides such a direct impact, the immigration of species from the south with new ecological needs and competitive traits will surely alter the structure of the feeding links, and thus give rise to changes in the benthic food web, the complex consequences of which are notoriously difficult to predict.

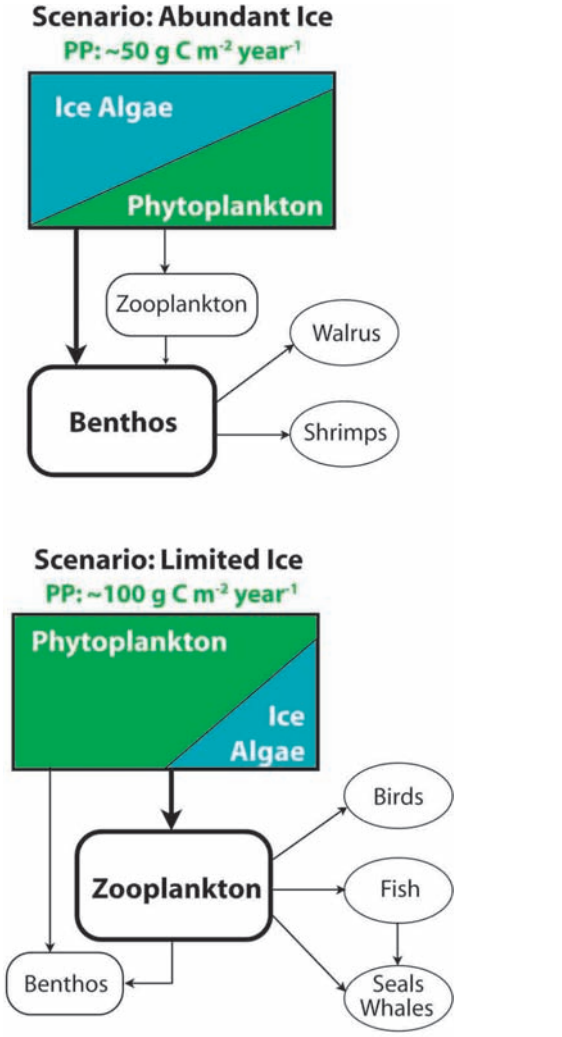

Fig. 2: Conceptual model of changes in the overall energy flux pattern through different trophic elements in sea ice, water column and seabed of Arctic seas, which are hypothesized to be related to the sea-ice decline caused by the rapid warming of the Arctic (after Carroll & Carroll 2003).

Abb. 2: Konzeptionelles Modell für Veränderungen im Energieflussmuster durch verschiedene trophische Kompartimente im Meereis, Pelagial und Benthal arktischer Meere, die durch den klimabedingten Rückgang des Meereises ausgelöst werden könnten (nach Carroll & Carroll 2003).

In conclusion, it is very obvious that the issue of the ecological consequences of climate change in Arctic seas is not settled and has so far not received the attention it actually deserves, facing the importance and urgency of the challenge to the scientific community. To address this issue, more long-term observations are necessary to gain time-series data on environmental and faunal variations, if possible at a decadal time scale, which is most significant to mankind. Another approach to investigate possible ecological effects of global change are strictly comparative case studies in Arctic "model" regions that are representative of different climate modes mentioned above ("cold / abundant ice" versus "warm / limited ice"). In addition, small-scale but multi-year investigations at selected sites in various habitats (coast, shelf, slope, and deep-sea), such as, e.g., the "Hausgarten" (Soltwedel et al. 2005), are needed to perform process-oriented work on the issue of how and to what extent environmental changes can affect benthic organisms and communities. Such studies will be greatly promoted by the latest progress in under-water and telecom-

munication technology that will result in an increaseing availability of autonomous and/or remotely-operated research platforms, either mobile and stationary, that will hopefully allow for a cost-effective and long-term observation and measurement of global-change effects in Arctic seafloor habitats.

In addition, a pan-Arctic perspective is needed to adequately address such a comprehensive issue. The discovery of the pronounced patchiness at local and regional scales strongly advises to take due caution in the spatial up-scaling of point-measurement results. It clearly hampers the sound generalization of the results and has to be adequately taken into account in budgeting and modelling attempts. A pan-Arctic approach is necessary to better understand the mechanisms responsible for the regional differences and to create an ample understanding of the emerging ecological changes. Such a broad-scale effort should comprise a network of international co-ordinated collaborative studies in different seas around the Arctic, applying highly standardized methodological approaches to ensure highest possible data comparability, and an appropriate organizational framework to foster subsequent data integration and modelling work.

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